F. J. Hardy[1], K. S. Shortreed[2], and J. G. Stockner[2]

Aquatic Environment Division
National Hydrology Research Centre
1 Environment Canada
11 Innovation Boulevard
Saskatoon, Saskatchewan
S7N 3H5

Department of Fisheries and Oceans
Fisheries Research Branch
2 West Vancouver Laboratory
4160 Marine Drive
West Vanvouver, B.C.
V7V 1N6

PLANKTON SIZE SPECTRA IN LAKES OF WESTERN CANADA

Unpublished Report

NHRI Contribution N. 88026

April 1988

Hardy, F.J., K.S. Shortreed, and J.G. Stockner. 1986. Plankton size spectra in lakes of western Canada. Can. J. Fish. Aquat. Sci. 00:000-000.

Plankton size spectra in 17 warm monomictic (nine dystrophic) coastal lakes in British Columbia are compared with data from 19 dimictic lakes in the Yukon Territory. During a portion of the study (1980-1984), a number of the monomictic lakes received whole-lake additions of inorganic nitrogen and phosphorus. Although picoplankton (<3 um) were the most abundant phytoplankton in all but unfertilized dystrophic lakes, their relative abundance decreased in clear monomictic lakes during nutrient addition while the relative abundance of microplankton (>20 um) increased. Cyanobacteria comprised 94% of the picoplankton in dimictic lakes, 96% of the picoplankton in unfertilized clear monomictic lakes, and 77% of the picoplankton in unfertilized dystrophic lakes. After nutrient addition, cyanobacteria comprised 93% of the picoplankton in clear monomictic lakes and 26% in dystrophic lakes. Microflagellate densities were greater in clear monomictic (treated and untreated) and treated dystrophic lakes than in dimictic or untreated dystrophic lakes; however, the relative abundance of microflagellates <20 um was similar in all lakes (82-87% of total microflagellate numbers). Zooplankton in the size range 0.16-0.85 mm were more abundant than small (<0.15 mm), large (0.86-1.5 mm) or larger (>1.5 mm) zooplankton in all lakes studied. Zooplankton abundance was generally much higher in dimictic lakes, and the zooplankton were of a larger size.

INTRODUCTION

Aspects of the ecology and size distribution of freshwater phytoplankton communities have been studied by numerous investigators for many years, but it was not until the recent development of techniques utilizing epifluorescent microscopy that the smallest portion of the phytoplankton community (algal picoplankton, 0.2-2.0 um) could be routinely enumerated (Chang 1980; Cronberg and Weibull 1981; Hickel 1981). Recent work on the distribution and abundance of algal picoplankton in the Laurentian Great Lakes has been reported (Caron et al. 1985; Munawar and Fahnenstiel 1982), but information on distribution of picoplankton in northwestern North America is limited to a discussion of phytoplankton carbon size spectra in some British Columbia lakes (Costella et al. 1979; Stockner 1987) and a description of picoplankton seasonal abundance in relation to nutrient reduction in Hobiton Lake, British Columbia (Hardy et al. 1986).

Biomass and size distribution of zooplankton are also important factors to consider if one is to understand the size-structure of phytoplankton communities. Abundances of microzooplankton (heterotrophic organisms ranging from 20-200 um) have often been underestimated in the past, primarily as a consequence of sampling technique limitations. Pace (1986) recently found that microzooplankton contribute approximately 40% of total zooplankton biomass in Quebec lakes and account for a significant portion of rates of community productivity, grazing, and nutrient regeneration. In addition, he presented evidence that size structure of zooplankton communities is independent of lake trophy, while

earlier studies (Brooks 1969; McNaught 1975) concluded that small zooplankton increase with eutrophication. Lake fertilization has shown conflicting results with regard to zooplankton size distribution: increases in micro-zooplankton (e.g. rotifers) were observed not only with nutrient addition (Nelson and Edmondson 1955; Donaldson et al. 1971) but also with nutrient reduction (Hardy et al. 1986). Other studies have documented increased zooplankton biomass with lake fertilization (LeBrasseur et al. 1978; Hyatt and Stockner 1985).

The Lake Enrichment Program (LEP) of the Department of Fisheries and Oceans has studied a number of British Columbia coastal and Yukon Territory lakes since 1977. These studies provide a unique opportunity for comparing plankton communities and their respective size spectra from both monomictic and dimictic lakes and for studying effects of nutrient additions on plankton communities (Stockner and Shortreed 1985; Shortreed and Stockner 1986). Monomictic lakes investigated in British Columbia are either clear or dystrophic and are oligotrophic as a result of low annual nutrient inputs and short water residence times (Stockner 1981). Whole-lake fertilization experiments with nitrogen (N) and phosphorus (P) have been conducted on several monomictic British Columbia lakes in efforts to enhance primary and secondary production and the growth and survival of planktivorous juvenile sockeye salmon (Oncorhynchus nerka) (LeBrasseur et al. 1978; Hyatt and Stockner 1985; Stockner 1987).

Hydrologic and climatic differences between coastal monomictic and interior dimictic lakes markedly affect the nutrient supply and attendant autotrophic response in each lake type. Hence, we might expect

differences in phytoplankton and zooplankton size spectra in each lake type and in lakes which have been nutrient enriched. The specific objectives of this study were: (1) to describe and compare the abundance and size spectra of phytoplankton and zooplankton in 19 dimictic lakes in the Yukon Territory with those in 17 monomictic British Columbia lakes, and (2) to compare the effects of nutrient additions on plankton size spectra in clear and dystrophic monomictic lakes.

DESCRIPTION OF STUDY LAKES

All but two dimictic lakes (Dezadeash and Sekulmun lakes) were located within the large Yukon River drainage basin in the south-central and southwestern portion of the Yukon Territory (Fig. 1). Lake elevations ranged from 579 to 1128 m above sea level (Table 1). The climate in this region is subarctic, with cool summers and long cold winters with annual average precipitation of <50 cm. Lake surface temperatures averaged 12°C in summer, and protracted periods of ice-cover usually occur from October-November to May-June. Lake areas ranged from 1.6 to 90 km^2, and mean depths ranged from 2.5 to 93 m while water residence times ranged from 1 to 22 yr.

The 17 monomictic lakes were located in the coastal zone of British Columbia (Fig. 1). Lake elevations ranged from 4 to 150 m above sea level (Table 1). The climate of this region is influenced by the Pacific Ocean and thus is cool Mediterranean, with cool, wet winters and warm dry summers. Lake surface temperatures averaged 14-20°C in summer and 4-6°C in winter, although short periods of ice cover occurred in some winters.

Lake areas ranged from 1.8 to 65 km^2, mean depths from 25 to 212 m, and water residence times from 0.2 to 7.3 yr. Of the 17 monomictic lakes included in this study, eight were clear (Great Central, Henderson, Hobiton, Kennedy, Long, Nimpkish, Sproat, and Woss lakes), and the remainder (Awun, Bonilla, Curtis, Devon, Eden, Ian, Lowe, Simpson, and Yakoun lakes) were mildly dystrophic. Twelve of the lakes were fertilized with inorganic N and P in some or all years of the study, and in one lake (Kennedy) which has two discrete basins, each basin was treated differently in each year (Stockner and Shortreed 1985).

METHODS

We sampled the Yukon Territory lakes monthly from June to September 1982 with a float-equipped Cessna 206 aircraft. Data from British Columbia lakes were collected between 1981 and 1984. Lakes were sampled from March-April to October-November (7 to 9 times $\cdot yr^{-1}$), usually from a DeHavilland Beaver aircraft. The monomictic British Columbia Lakes were either clear or dystrophic and were divided into untreated or treated categories. The two untreated dystrophic monomictic lakes are typical examples of this lake type and represent a valuable comparison with treated dystrophic lakes despite the small sample size. Results are reported as growing season averages, defined as the period when surface temperatures reach 8°C in spring until they decrease from summer maxima to 12°C in fall.

An aqueous solution of ammonium nitrate and ammonium phosphate was used to fertilize the British Columbia lakes in an N:P atomic ratio of

15:1, except in 1982 and 1983 in Kennedy Lake (Clayoquot Arm), when the N:P ratio was 26:1 and 35:1, respectively (Stockner and Shortreed 1985). Fertilizer was applied once weekly using a DC-6B water bomber for a period of 19-26 wk commencing in April-May (Stephens and Stockner 1983). When fertilizer was applied, lakes were sampled 2 to 4 d after application.

Temperature profiles to a depth of 50 m were obtained with a Montedoro-Whitney temperature probe (model TC-5C). Buoyancy frequencies (Turner 1973) were calculated from temperature data and were used to determine epilimnion depth. A Li-Cor light meter (model 185A) equipped with an underwater quantum sensor (model 192S) was used to measure photosynthetically active radiation (400-700 nm) from the water surface to depths where light intensity was 1% of surface values. We used light data to calculate vertical extinction coefficients (k) and compensation depths.

A 6-L, opaque Van Dorn bottle was used to obtain water samples from three epilimnetic and one hypolimnetic depths. Two 2-L polyethylene bottles and one glass culture tube were filled with water from each depth. Samples were preserved within 4 h of collection, and all subsequent chemical analyses were carried out with the methods of Stephens and Brandstaetter (1983) as described in detail by Stockner and Shortreed (1985) and Shortreed and Stockner (1986).

Samples of chlorophyll _a_ determinations were collected by filtering 0.5 L of water from each depth through a 0.8-um, 47-mm diameter Millipore AA filter. Filters were placed in foil dishes, dried in a desiccator,

and frozen. Samples were macerated in 90% acetone and analyzed with a Turner model III fluorometer.

Samples for phytoplankton enumeration and identification were collected from 1, 3, 5, and 30 m depth, placed in opaque, 125-mL polyethylene bottles, and transported to the field laboratory. In this study, we follow the convention of Sieburth et al. (1978) and define picoplankton as cells <3 um, nanoplankton as cells 3-20 um, and microplankton as cells from 20-200 um. Picoplankton were preserved according to methods described by MacIsaac and Stockner (1985) and counted at 1250 X magnification with a Zeiss compound microscope (Model KLSM) equipped with a IV/FL epifluorescent condenser, HBO 50-W mercury lamp, LP 397 and KP 560 exciter filters, FT 580 beam splitter, and LP 590 barrier filter. Random fields were counted until a minimum of 200 cells or 30 fields were counted. Unfiltered water from each depth was fixed with 1 ml of Lugol's acid solution and used for enumeration of nano- and microplankton. Additionally, microflagellates (2-20 um) and flagellates (>20 um) were enumerated from this sample. Samples were shaken and settled overnight in 7-, 12-, or 27-mL settling chambers and one transect at 187.5 X and one transect at 750 X magnification were counted with a Wild M40 inverted microscope equipped with phase contrast optics. Maximum dimensions of each identified species were determined using a calibrated eyepiece micrometer. We used modified equations from Strathmann (1967) to estimate the carbon content of phytoplankton, expressed here as $mgC \cdot m^{-3}$.

Zooplankton were collected at every station with a 100-um mesh size SCOR-UNESCO net (mouth area = 0.25 m^2) which was hauled vertically at approximately 0.5 $m \cdot s^{-1}$ from 50 m to the surface. Zooplankton were preserved in a borax-buffered, 4% formalin-sucrose solution (Haney and Hall 1973). In the laboratory each sample was halved with a Folsom plankton splitter. One portion was filtered onto an ashed and weighed Whatman GFC filter, dried to a constant weight at 90°C for 24 h, and weighed. Zooplankton biomass was expressed as mg dry weight $\cdot m^{-3}$. The other portion of the sample was used for zooplankton identification and enumeration with a microcomputer based caliper system (Sprules et al. 1981).

A single factor ANOVA was run for each variable to test for differences between means (Zar 1974). Because the sample size was small, untreated dystrophic lakes were not included in the ANOVA. If the ANOVA rejected a multisample hypothesis of equal means, the Newman-Keuls multiple range test for unequal sample sizes was used to detect differences between all the pairs of means.

RESULTS AND DISCUSSION

Dimictic lakes

The clear dimictic Yukon Territory lakes we investigated receive peak flows and nutrient inputs in spring as snow and ice melt and as light intensity, surface temperature, and water column stability are rapidly increasing. Average summer total phosphorus concentrations range from 3-13 ug$P \cdot L^{-1}$, average total nitrogen concentrations from 213-822

$ugN \cdot L^{-1}$, and average dissolved silicon concentrations from 610-4300 $ug \cdot L^{-1}$ (Shortreed and Stockner 1986). Due to differing hydrologic regimes of coastal monomictic and interior dimictic lakes, the proportion of annual nutrient load biologically utilized is far greater in the dimictic lakes (Stockner and Shortreed 1985).

Significantly higher phytoplankton concentrations ($p<.025$) were observed in Yukon lakes than in untreated clear monomictic lakes of the British Columbia coast and were due principally to geomorphological and hydrological conditions which impart longer water residence times and higher concentrations of nutrients (Fig. 2). However, estimates of phytoplankton biomass (both as carbon and chlorophyll) were not significantly higher in dimictic Yukon lakes than in untreated monomictic lakes (Figs. 3, 4). Most carbon in all lake types was in the microplankton fraction, and in dimictic lakes, microplankton contributed 56% of total phytoplankton carbon (Fig. 3). Since the equations of Strathmann (1967) generally overestimate the carbon content of large vacuolated diatoms and since the large diatom Rhizosolenia spp. was abundant in many of our monomictic study lakes, carbon content of the microplankton is likely overestimated (Shortreed and Stockner 1986), thereby contributing to discrepancies between estimates of phytoplankton biomass and abundance.

Picoplankton were the most abundant phytoplankton in Yukon lakes (75% of total phytoplankton numbers), and densities were significantly higher ($p<.001$) in these dimictic lakes than in other lake types (Fig. 2). Procaryotic cyanobacteria, primarily a phycoerythrin-rich form of

Synechococcus, comprised 94% of total picoplankton in dimictic lakes, with eucaryotes (Chlorella-like forms) comprising the remainder (Fig. 5). Although a considerable number of North American lakes remain uninvestigated for picoplankton (Stockner and Antia 1986), our observations substantiate previous reports of cyanobacterial ubiquity in freshwater as well as oceanic systems. In North America, cyanobacterial picoplankton have been found in Lake Ontario (Caron et al. 1985), Lake Superior (Munawar and Fahnenstiel 1982), a Michigan lake (Lehman and Sandgren 1982), a small meromictic lake in Ontario (Craig 1984), eight north-central Minnesota lakes (Fliermans and Schmidt 1977), and freshwater enclosures in Cuba (Komarek 1985).

Relative abundances of two size categories of microflagellates (<20 um and >20 um) were similar in all lake types (Fig. 6). The smaller size fraction comprised 82-87% of total microflagellate numbers, which is not surprising considering the extreme oligotrophic condition of these lakes and the high densities of small algal and bacterial picoplankton that can serve as food for heterotrophic microflagellates (Caron et al. 1985). Lower absolute densities of microflagellates in Yukon lakes than in British Columbia coastal lakes may be due to a much higher abundance of zooplankton which graze microflagellates.

Zooplankton were divided into four size categories (<0.15 mm, 0.16-0.85 mm, 0.86-1.5 mm, >1.5mm)(Fig. 7, Tables 2, 3). Most zooplankton in all lake types were in the medium size range (0.16-0.85 mm). Greatest abundances and most very large zooplankton were observed in dimictic Yukon lakes, where the main species were Cyclops scutifer,

Daphnia spp., and Diaptomus pribilofensis. The very high abundances of zooplankton in Yukon lakes are attributed not only to a higher trophic status than the British Columbia coastal lakes but also to much lower densities of planktivorous fish than occur in the coastal lakes (Lindsey et al. 1981; Shortreed and Stockner 1986).

Dystrophic monomictic lakes

Our monomictic British Columbia coastal lakes are clear or dystrophic and have low annual nutrient inputs and short water residence times (Table 1). Their maximum water input and nutrient loading occur in winter when light intensity, water temperature, and water column stability are low; consequently, nutrient concentrations tend to be very low. The more northerly coastal lakes are slightly acidic and generally more dystrophic with shallower euphotic zones. Average summer total phosphorus and total nitrogen values are generally lower in the monomictic than in the dimictic lakes: 1-2 $ugP \cdot L^{-1}$ and 120-266 $ugN \cdot L^{-1}$ in untreated lakes, 1-7 $ugP \cdot L^{-1}$ and 118-395 $ugN \cdot L^{-1}$ in treated lakes (Stockner and Shortreed 1985). Silicon concentrations range from 0.12-2.20 $mg \cdot L^{-1}$, which indicate that silicon limitation is unlikely to be a factor regulating chrysophyte production in British Columbia lakes except at certain periods in certain lakes (Stockner and Shortreed 1985).

Phytoplankton abundance was markedly lower in untreated dystrophic coastal lakes than in other lake types. However with treatment, phytoplankton abundance in dystrophic lakes was not significantly

different ($p>.50$) than in untreated coastal clear lakes (Fig. 2, Table 2). Furthermore, nutrient additions more than doubled chlorophyl. and phytoplankton carbon in dystrophic and clear monomictic lakes (Figs. 3, 4). The paucity of phytoplankton in dystrophic lakes relative to clear coastal lakes is due to several factors. These northern dystrophic systems have shorter growing seasons, reduced compensation depths, and generally cooler epilimnetic temperatures (Stockner 1987). Planktivore densities also tend to be lower in dystrophic lakes, permitting larger populations of zooplankton of larger mean size (e.g. Daphnia) to occur, with subsequent higher grazing pressure on the phytoplankton community. The reverse is true for clear coastal lakes, where planktivore densities are higher, larger zooplankton are less abundant, and phytoplankton are more abundant.

Picoplankton were the most abundant phytoplankton in all lake types except in untreated dystrophic lakes, where microplankton were more common (Fig. 2). Numbers of picoplankton were lowest in dystrophic lakes, and, of total phytoplankton, comprised only 33% in untreated and 59% in treated dystrophic lakes. This increase in abundance represented the greatest relative increase in any plankton size group with fertilization (Figs. 2, 5). Small cells tend to have higher uptake rates and shorter doubling times than larger cells (Lehman and Sandgren 1984), and hence are expected to be one of the first phytoplankton size fractions in these oligotrophic lakes to respond to nutrient additions. Eucaryotic picoplankton (Chlorella-like forms) were the main forms to increase with fertilization in the acidic dystrophic lakes (Fig. 5). In

untreated and treated dystrophic lakes, only 77% and 26% of picoplankton were procaryotic, respectively, compared to 93-96% of total picoplankton in dimictic and clear monomictic lakes. Lower numbers of procaryotic picoplankton in the slightly acidic dystrophic lakes may be the result of a preference for more alkaline conditions by Synechococcus (Waterbury et al. 1979).

Lower densities of total microflagellates were observed in unfertilized dystrophic lakes than in other monomictic lakes, due in part to a higher relative abundance of zooplankton to phytoplankton in dystrophic lakes (Fig. 6). Zooplankton data by size were unavailable for untreated dystrophic lakes, but in treated dystrophic lakes, most zooplankton were of medium size (0.16-0.85 mm)(Fig. 7). Common zooplankton species found in dystrophic monomictic lakes were Eubosmina coregoni, Cyclops vernalis, Diaphanosoma sp., Diacyclops bicuspidatus, Holopedium gibberum, Daphnia longiremis, Epischura nevadensis, and Kellicottia spp.

Clear monomictic lakes

Phytoplankton abundances were significantly lower ($p<.025$) in clear untreated monomictic lakes of the British Columbia coast than in dimictic lakes of the Yukon Territory (Fig. 2), and nutrient additions more than doubled chlorophyll and phytoplankton carbon in clear monomictic lakes (Figs. 3, 4). In treated clear monomictic lakes, highest concentrations of phytoplankton carbon and greatest densities of large diatoms occurred. Consequently, most carbon was in the microplankton fraction.

If microplankton carbon is not included in the carbon estimate because of potential overestimation due to vacuolated species like Rhizosolenia, two to six times more phytoplankton carbon occurred in the pico-nanoplankton in fertilized clear lakes than in the other lake types.

Picoplankton comprised 79% of total phytoplankton abundance in untreated clear coastal lakes, and their numbers increased with nutrient addition. As in the dimictic Yukon lakes, most of the picoplankton were procaryotic Synechococcus (Fig. 5).

Total microflagellate densities were significantly greater in both treated ($p<.005$) and untreated ($0.1<p<0.2$) clear monomictic lakes than in dimictic Yukon lakes (Fig. 6). Microflagellate abundance increased in all treated lakes, most likely a result of increased densities of pico- and nano- phytoplankton as food for heterotrophic microflagellates as well as increased nutrient supply for phototrophic microflagellates. Recent observations from Sproat Lake indicate that abundance of both phototrophic and heterotrophic microflagellates increased following nutrient addition (J. Hardy, unpublished data).

Zooplankton abundances were significantly lower in monomictic clear lakes than in dimictic lakes ($p<.001$)(Fig. 7). The relatively low abundances of zooplankton in the coastal British Columbia lakes are a result of low ambient nutrient levels and high densities of planktivorous fish, especially juvenile sockeye salmon. Common zooplankton in clear monomictic lakes were the same as in dystrophic monomictic lakes, and their abundance did not increase as a result of treatment. Slightly lower abundances of small zooplankton (mostly rotifers) were observed in

treated as opposed to untreated clear monomictic lakes, a result similar to observations in Hobiton Lake, British Columbia, where rotifers and small zooplankton were less abundant during nutrient addition (Hardy et al. 1986). Medium size zooplankton (0.16-0.85 mm) were also slightly less abundant in treated than in untreated clear monomictic lakes, while the abundance of larger zooplankton (>0.86) was unchanged with nutrient addition.

LeBrasseur and Kennedy (1972) reported marked increases in zooplankton biomass rather than zooplankton numbers in Great Central Lake during the first year of treatment compared to the previous untreated year. Increases in zooplankton biomass with nutrient additions were also observed in several other British Columbia coastal lakes (Kennedy Clayoquot Arm 1978; Kennedy Main Arm 1979; Curtis 1980; Bonilla 1980; Long 1982; Morice 1980)(Hyatt and Stockner 1985). When we compare zooplankton biomass (dry weight) rather than abundance in the lakes currently described, increases were observed in dystrophic (14.8 $mg \cdot m^{-3}$ pretreatment, 19.7 $mg \cdot m^{-3}$ treatment) and clear (5.7 $mg \cdot m^{-3}$ pretreatment, 8.5 $m \cdot m^{-3}$ treatment) monomictic lakes following nutrient addition. Zooplankton biomass (dry weight) may include filamentous algae that increased in abundance with treatment, hence previous reports of increased zooplankton biomass may be in error. Furthermore, increased microplankton abundance with fertilization may have resulted in decreased net efficiency thereby masking any zooplankton increases. Unfortunately, additional problems associated with the measurement of biomass of micro- and macrozooplankton (e.g. Pace 1986)

place constraints on the confidence associated with estimates of zooplankton biomass by size, an alternative method of determining total zooplankton biomass.

In Hobiton Lake, greatest densities of the cladocerans Diaphanosoma and Eubosmina were observed in a year of nutrient addition, and small zooplankton (rotifers) were most dense following nutrient reduction (Hardy et al. 1986). Cladocerans have been shown to inhibit the population growth of rotifers by both exploitive and interference competition (Gilbert 1985; Gilbert and Stemberger 1985) and, in years of treatment, may reduce rotifer populations. An alternative explanation for the slight shift in zooplankton size distribution with nutrient addition may be increased grazing pressure by fish. Such a shift to small zooplankton in the presence of increased grazing pressure has been observed in coastal British Columbia lakes (O'Neill and Hyatt 1987).

ACKNOWLEDGMENTS

The assistance of M. Turner, H. Spence, L. Soukup, and K. Masuda with data analyses and B. Nidle with preparation of the figures is greatly appreciated. We thank E. Prepas for useful comments on the manuscript. Funding was provided by the Visiting Fellowship Program of the Natural Sciences and Engineering Research Council of Canada (NSERC).

REFERENCES

Brooks, J. L. 1969. Eutrophication and changes in the composition of zooplankton, p. 236-255. In Eutrophication: Causes, consequences, correctives. Natl. Acad. Sci.

Caron, D. A., F. R. Pick, and D. R. S. Lean. 1985. Chroococcoid cyanobacteria in Lake Ontario: vertical and seasonal distributions during 1982. J. Phycol. 21: 171-175.

Chang, V. T.-P. 1980. Zwei neue Synechococcus-Arten aus dem Zurichsee. Schweiz. Z. Hydrol. 42: 247-254.

Craig, S. R. 1984. Productivity of algal picoplankton in a small meromictic lake. Verh. Internat. Verein. Limnol. 22: 351-354.

Cronberg, G., and C. Weibull. 1981. Cyanodictyon imperfectum, a new chroococcal blue-green alga from Lake Trummen, Sweden. Arch. Hydrobiol. Suppl. 60: 101-110.

Donaldson, L. R., P. R. Olson, S. Olsen, and Z. F. Short. 1971. The Fern Lake Studies. Univ. Wash. Coll. Fish. Contrib. No. 352: 76 p.

Fenchel, T. 1984. Suspended marine bacteria as a food source, p. 301-315, In: M. R. Fasham (ed.). Flows of energy and material in marine ecosystems - theory and practice. Plenum Press, New York.

Fliermans, C. B., and E. L. Schmidt. 1977. Immunofluorescence for autoecological study of a unicellular blue-green alga. J. Phycol. 13: 364-368.

Gilbert, J. J. 1985. Competition between rotifers and Daphnia. Ecology 66(6): 1943-1950.

Gilbert, J. J., and R. S. Stemberger. 1985. Control of Keratella populations by interference competition from Daphnia. Limnol. Oceanogr. 30(1): 180-188.

Haney, J. F., and D. J. Hall. 1973. Sugar-coated Daphnia: a preservation technique for Cladocera. Limnol. Oceanogr. 18(2): 331-333.

Hardy, F. J., K. S. Shortreed, and J. G. Stockner. 1986. Bacterioplankton, phytoplankton, and zooplankton communities in a British Columbia coastal lake before and after nutrient reduction. Can. J. Fish. Aquat. Sci. 43: 1504-1514.

Hickel, B. 1985. Cyanonephron styloides gen. et sp. nov., a new chroococcal blue-green alga (Cyanophyta) from a brackish lake. Arch. Hydrobiol. (S): 71: 99-104.

Hyatt, K. D., and J. G. Stockner. 1985. Responses of sockeye salmon (Oncorhynchus nerka) to fertilization of British Columbia coastal lakes. Can. J. Fish. Aquat. Sci. 42: 320-331.

Komarek, J. 1985. Do all cyanophytes have a cosmopolitan distribution? Survey of the freshwater cyanophyte flora of Cuba. Arch. Hydrobiol. (S): 71: 359-386.

LeBrasseur, R. J., C. D. McAllister, W. E. Barraclough, O. D. Kennedy, J. Manzer, D. Robinson, and K. Stephens. 1978. Enhancement of sockeye salmon (Oncorhynchus nerka) by lake fertilization in Great Central Lake: summary report. J. Fish. Res. Board Can. 35: 1580-1596.

Lehman, J. T., and C. D. Sandgren. 1982. Phosphorus dynamics of the procaryotic nannoplankton in a Michigan lake. Limnol. Oceanogr. 27(5): 828-838.

Lindsey, C. C., K. Patalas, R. W. Bodaly, and C. P. Archibald. 1981. Glaciation and physical, chemical, and biological limnology of Yukon lakes. Can. Tech. Rep. Fish. Aquat. Sci. No. 966: 45 p.

MacIsaac, E. A., and J. G. Stockner. 1985. Current trophic state and potential impacts of coal mine development on productivity of Middle Quinsam and Long lakes. Can. Tech. Rep. Fish. Aquat. Sci. 1381: 63 p.

McNaught, D. C. 1975. A hypothesis to explain succession from calanoids to cladocerans during eutrophication. Int. Ver. Theor. Angew. Limnol. Verh. 19: 724-731.

Munawar, M., and G. L. Fahnenstiel. 1982. The abundance and significance of ultraplankton and microalgae at an offshore station in Central Lake Superior. Can. Tech. Rep. Fish. Aquat. Sci. 1153: 1-13.

Nelson, P. R., and W. T. Edmondson. 1955. Limnological effects of fertilizing Bare Lake, Alaska. Fish. Bull. 56(102): 415-436.

O'Neill, S. M. and K. D. Hyatt. 1987. An experimental study of competition for food between sockeye salmon (Oncorhynchus nerka) and threespine stickleback (Gasterosteus aculeatus) in a British Columbia coastal lake. Can. J. Fish. Aquat. Sci. Spec. Publ. (in press).

Pace, M. L. 1986. An empirical analysis of zooplankton community size structure across lake trophic gradients. Limnol. Oceanogr. 31(1): 45-55.

Shortreed, K. S., and J. G. Stockner. 1986. Trophic status of 19 subarctic lakes in the Yukon Territory. Can. J. Fish. Aquat. Sci. 43: 797-805.

Sieburth, J. McN., V. Smetacek, and J. Lenz. 1978. Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnol. Oceanogr. 23: 1256-1263.

Sprules, W. G., L. B. Holtby, and G. Griggs. 1981. A microcomputer-based measuring device for biological research. Can. J. Zool. 59: 1611-1614.

Stephens, K., and R. J. Brandstaetter. 1983. A laboratory manual, collected methods for the analysis of water. Can. Tech. Rep. Fish. Aquat. Sci. 1159: 68 p.

Stephens, K., and J. G. Stockner. 1983. The lake fertilization program: methods for the fertilization of lakes in British Columbia 1970 to 1982. Can. Tech. Rep. Fish. Aquat. Sci. 1192: 51 p.

Stockner, J. G. 1981. Whole-lake fertilization for the enhancement of sockeye salmon (Oncorhynchus nerka) in British Columbia, Canada, Verh. Int. Ver. Limnol. 21: 293-299.

Stockner, J. G. 1987. Lake fertilization: the enrichment cycle and lake sockeye production. Can. J. Fish. Aquat. Sci. Spec. Publ. (in press).

Stockner, J. G. and N. J. Antia. 1986. Algal picoplankton from marine and freshwater ecosystems: a multidisciplinary perspective. Can. J. Fish. Aquat. Sci. 43: 2472-2503.

Stockner, J. G., and K. S. Shortreed. 1985. Whole-lake fertilization experiments in coastal British Columbia lakes: empirical relationships between nutrient inputs and phytoplankton biomass and production. Can. J. Fish. Aquat. Sci. 42: 649-658.

Strathmann, R. R. 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. 12: 411-418.

Turner, J. S. 1973. Buoyancy effects of fluids. Cambridge Press, Cambridge. 367 p.

Vincent, W. F. 1982. Autecology of an ultraplankton shade alga in Lake Tahoe. J. Phycol. 18: 226-232.

Waterbury, J. B., S. W. Watson, R. R. L. Guillard, and L. E. Brand. 1979. Widespread occurrence of a unicellular, marine, planktonic cyanobacterium. Nature. 277: 293-294.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc. 620 pp.